Евразиатский энтомол. журнал 14(2): 134–138

Is *Triodia nubifer* (Lepidoptera, Hepialidae) the only pre- or interglacial relic species of Lepidoptera in the Altai-Sayan Mountain System?

Является ли *Triodia nubifer* (Lepidoptera, Hepialidae) единственным до- или межледниковым реликтом среди чешуекрылых в горах Алтае-Саянской горной страны?

V.V. Dubatolov*, O.E. Kosterin, *****
В.В. Дубатолов*, О.Э. Костерин, *****

* Institute of Systematics and Ecology of Animals SB RAS, Frunze Str. 11, Novosibirsk 630091 Russia. E-mail: vvdubat@mail.ru.
* Институт систематики и экологии животных СО РАН, ул. Фрунзе 11, Новосибирск 630091 Россия.

** Institute of Cytology and Genetics SB RAS, Academician Lavrentiev Ave. 10, Novosibirsk 630090 Russia. E-mail: kosterin@bionet.nsc.ru
** Институт цитологии и генетики СО РАН, пр. ак. Лаврентьева 10, Новосибирск 630090 Россия.

*** Novosibirsk State University, Pirogova Str. 2, Novosibirsk, 630090 Russia.
*** Новосибирский государственный университет, ул. Пирогова 2, Новосибирск 630090 Россия.

Key words: Lepidoptera, Hepialidae, *Triodia nubifer*, Altai, glaciation, climatic optimum, isolation.

Ключевые слова: Lepidoptera, Hepialidae, чешуекрылые, тонкопряды, *Triodia nubifer*, Алтай, оледенение, климатический оптимум, изоляция.

Abstract. Earlier we supposed that relatively thermophylous nemoral and subnemoral Lepidoptera species could not survive during the Pleistocene climate coolings in Altai. Presence in the Altai foothills and Gornaya Shoria Mts. of an endemic Hepialidae species, *Triodia nubifer* (Lederer, 1853), challenges this statement. We suppose that extinctions during the Pleistocene climate coolings first of all concerned those nemoral insect species which developed openly on plants while species with ground-dwelling larvae, as in *T. nubifer*, could survive. This view is supported by presence in the Altai foothills of endemic subnemoral pedobiotic species in other groups, such as ground beetles and ground worms.

Резюме. Ранее было сделано предположение, что теплолюбивые неморальные и субнеморальные виды чешуекрылых не могли выжить во время плейстоценовых оледенений в горах Алтая. Присутствие в предгорьях Алтая и в Горной Шории эндемичного вида чешуекрылых —тонкопрядов (Hepialidae), *Triodia nubifer* (Lederer, 1853), на первый взгляд, противоречит этому утверждению. Мы предполагаем, что вымиранию во время плейстоценовых похолоданий должны были подвергаться прежде всего те неморальные виды насекомых, которые открыто развиваются на растениях. Напротив, виды со скрытноживущими в почве гусеницами, как у *T. nubifer*, могли выживать. Это предположение поддерживается обитанием в предгорьях Западного Алтая субнеморальных геобионтных видов в других группах животных, например, среди дождевых червей.

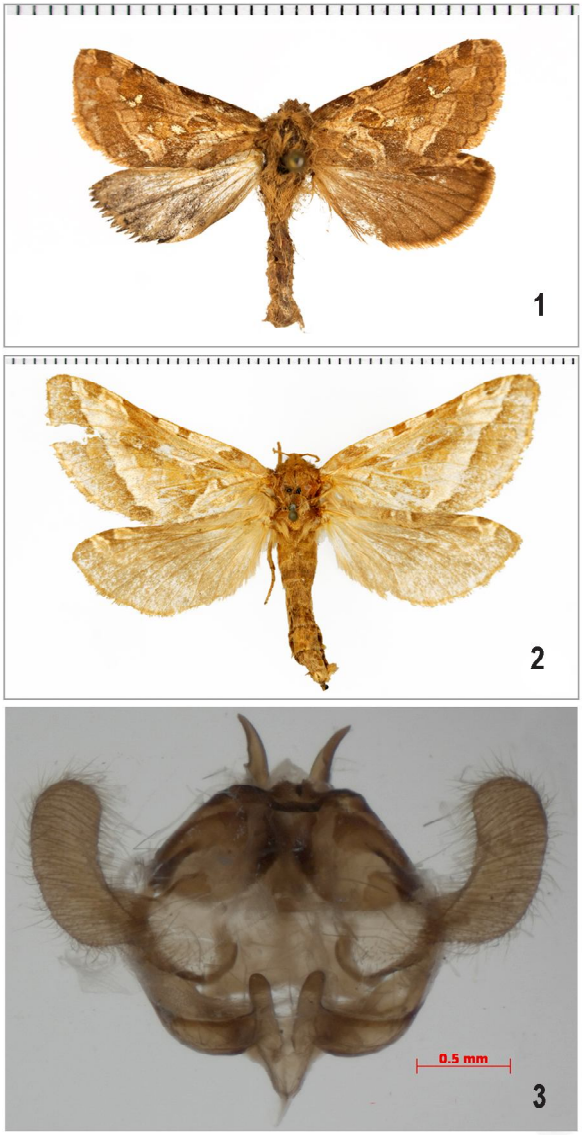
Intriduction

In 2010 –2011, Dubatolov and Knyazev [2011] undertook a study of distribution and morphology of a little-known representative of the Hepialidae family described from West Altai, *Triodia nubifer* (Lederer, 1853) (Fig. 1–3). This species has been first collected by A. Kindermann in West Altai foothills, between Ust'-Kamenogorsk and Ust'-Bukhtarminsk (Kazakhstan) and described in the first paper devoted to Lepidoptera of Altai [Lederer, 1853]. Although *T. nubifer* was included into all relevant catalogues and atlases of early XX century, its diagnostic characters, generic attribution, position in the genus and the range remained unclear. Only one and half century after description, Nielsen et al. [2000] studied the type series and attributed the species to the genus *Triodia* Hübner, [1820]. Dubatolov, Knyazev [2011] clarified the species range and described in detail its morphological characters and differences from related species, which were not considered by Nielsen et al. [2000].

The results of this study lead us to a supposition that this species is the only subnemoral lepidopteran in Altai which does not fit the hypothesis of their relatively recent recolonization [Dubatolov, Kosterin, 2000]. This point of view is substantiated below.

Subnemoral species of Lepidoptera in Siberia in the context of the problem of the classification and origin of Siberian forests

Consideration of coenotic connection of *T. nubifer* is difficult because of the lack of unified classification of Siberian forests and internationally accepted nomenclature of their types. Generally, an international reader is not familiar with vegetation of the vast territory of Siberia, which is quite peculiar.



Figs 1–3. *Triodia nubifer* (Lederer), topotypes, male (1) and female (2), from coll. Eversmann in Zoological Institute, St.-Petersburg, Russia; male genitalia (3), Russia, Altaiskii Krai, Krasnostshekovo.

Рис. 1–3. *Triodia nubifer* (Lederer), топотипы, самец (1) и самка (2), из коллекции Э. Эверсманна, Зоологический институт, Санкт-Петербург, Россия; гениталии самца (3), Россия, Алтайский край, Красношёково.

The term «nemoral» refer to plant and animals species associated with broad-leaved forests of the temperate zone of Northern Hemisphere. However, not all trees called broad-leaved in English can be considered nemoral. Such trees as birch, poplars (mostly aspen, *Populus tremula*) and willows co-exist with conifers as subdominants in the boreal zone and may exclude them completely. As well as conifers, they are usually considered among boreal tree species and in Russian literature are often called «small-leaved trees» (in spite of their leaves not necessarily being small), while the term «broad-leaved» is reserved for truly nemoral (temperate) trees and forests of oaks, ashes, elms, lindens, hornbeams, etc. [reviewed in: Dubatolov, Kosterin, 2000]. The forests of Siberia are almost exclusively represented by coniferous or taiga forests, mixed coniferous/birch(/aspen) and, in the south, pure birch/aspen forests. The two latter forest types were recently very broadly classified, in a geographical sense, as hemiboreal forests, to distinghush them from the boreal forests *per se* (taiga) [Ermakov et al., 2000], although their boreal floristic component is actually very scarce, if any (N.N. Lashchinskiy, pers. comm.) . The nemoral broad-leaved (temperate) trees are either absent from Siberia or confined to very few relic isolates [Dubatolov, Kosterin 2000; Koropachinskiy, Vstovskaya, 2002]. Presently the Altai-Sayan Mountain System completely lacks such broad-leaved trees as oaks, ashes, hornbeams, alder (except for the bushy *Dushekia fruticosa* which is not nemoral and is present in high mountains). Elms are represented by *Ulmus pumila* s.l. forming groves only in southern, steppe-desert foothills. Linden (*Tilia sibirica*) forests are found only in an isolate in Gornaya Shoria Mts. in Kemerovo Province, colloquially known as «the linden island» [Kuminova, 1951, 1957, 1960; Khlonov, 1965; Ermakov, 1998; Ermakov et al., 2000; Novák et al., 2014]; besides, linden occurs as an admixture to mixed forests near Krasnoyarsk. The so-called «chernevaya taiga», with domination of Siberian fir (*Abies sibirica*) and aspen (*Populus tremula*), which occupies the most humid western foothills of Altai Mts. and Kuznetskoe Upland (including Gornaya Shoria Mts. where it embraces patches of linden forests) is considered a direct derivative and ecological analog of nemoral forest communities and was termed subnemoral forest [Ermakov, 1998]. (In a recent paper by Novák et al. [2014], chernevaya tayga and the Shorian linden forests are considered broadly among hemiboreal forests, although they completely miss boreal species in herbage, while the Siberian fir can hardly be called a boreal species as well).

Since mid–XX century, some thermo- and hygrophilous species of plants and animals presently existing in the Altai-Sayan Mountain System in isolation from their main ranges have been repeatedly supposed to be «Tertiary relicts» persisting in these places since the Tertiary Period [Kuminova, 1951, 1957, 1960; Peshkova 1984; Polozhii, Krapivkina, 1985; Belyshev, Haritonov, 1978, 1981; Mikkola, 1987]. Thus, Kuminova [1951, 1957] attracted attention to a number of nemoral species of herbaceus plants (such as *Asarum europaeum* L., *Asperula odorata* L., *Circaea lutetiana* L., *Festuca gigantea* (L.) Vill., etc.) occurring, as well as linden, in the Kuznetsk Upland in isolation from their main European ranges and supposed them to exist there since preglacial times [Khlonov, 1965]. Walter and Straka [1970] supposedly dated these isolate to the last interglaciation, and only Reverdatto [1940] supposed these nemoral species to reach their current Siberian isolated position as recently as in the Holocene. It is noteworthy that the mentioned areas are free from animal species obligatorily connected to

nemoral forests. The Lepidoptera species which may be called subnemoral inhabiting western and northern foothills of the Altai-Sayan Mountain System have been reviewed by Dubatolov, Kosterin [2000]. In the cited work, arguments have been put forward that these species could not have survived the Pleistocene climate coolings in this region *in situ*:

— (i) environment of the open taiga/cryophyte forest-steppe as reconstructed for the region for the glacial times by paleopalinological methods was too harsh for such relatively thermophylous species, and
— (ii) there are no species endemic for this area among nemoral and subnemoral Lepidoptera; some species are represented by endemic subspecies at most (like *Limenitis helmanni helmanni* Lederer, 1853, *L. sydyi sydyi* Lederer, 1853, *Mellicta plotina standeli* Dubatolov, 1997, *Acronicta major atritaigensa* Dubatolov et Zolotarenko, 1996).

Therefore, the species considered should have arrived to the Altai-Sayan Mountain System in postglacial time, the Holocene. The Altai-Sayan isolates of some subnemoral species were supposed to be remnants of the contiguous trans-Siberian ranges which existed at the Atlantic time (the so-called climatic Optimum of the Holocene) about 8 thousand years ago [Dubatolov, Kosterin, 2000]. It is noteworthy that during last decades, West Siberia has been colonized from the west by additional subnemoral species: *Maniola jurtina* (Linnaeus, 1758) [Knyazev, Kosterin, 2003; Kosterin et al., 2007], *Argyronome laodice* (Pallas, 1771) [Kosterin et al., 2007], and *Apatura iris* (Linnaeus, 1758) [Kosterin et al., 2007; Ivonin et al., 2012], the latter having penetrated up to the north-western Altai [Yakovlev et al., 2014]. This colonization is most probably being driven by the recent climate warming, thus showing how fast southern West Siberia may become enriched with subnemoral lepidopteran species.

Triodia nubifer as a subnemoral species

The range of *Triodia nubifer* is restricted to the foothills of West Altai and the so-called «linden island» of Gornaya Shoria Mts (Fig. 4) [Dubatolov, Knyazev, 2011] (Fig. 4). This is exactly the territory where Kuminova [1951] revealed elements of herb and bush flora of the European nemoral forests. Most of the *T. nubifer* range is occupied by the subnemoral fir/aspen «chernevaya taiga», while in «the linden island» nearly pure stands of linden occur. So, *T. nubifer* is pertained to most warm and humid areas of the mountain system and may be characterized as subnemoral, rather thermo- and hydrophilic species.

Timing of the arrival of the ancestors of *T. nubifer* to its recent range

In its morphology, *T. nubifer* quite differs from other species of the genus *Triodia* Hübner, [1820] and has no close relatives [Dubatolov, Knyazev, 2011]. Most of other representatives of the genus, forming several species groups, range from Balkans in South-Eastern Europe via Asia Minor and the Caucasus to Western Kopetdagh Mts. in Turkmenistan and probably to Uzbekistan (Fergana); only the type species *T. sylvina* (Linnaeus, 1761), enjoys west-central Palaearctic distribution from England and Spain east to Lake Baikal [de Freina, Witt, 1990; Sinev, Zolotuhin, 2008].

Formation of a new species is thought to take not less than 1,000–50,000 years [Zimmerman, 1960; Clarke et al., 2001]. However, the known species of *Triodia* differ substantially among each other (including from *T. nubifer*) in the genitalia structure, at the level corresponding to that observed in a number of vicariant East-Asian/North American pairs of nemoral Lepidoptera species which have diverged not later than the Pliocene [Dubatolov, Kosterin, 2000]. Very preliminarily, we may estimate the time of divergence of *Triodia* species as not less than one million years ago, that is the warm and humid time when the ancestor of *T. nubifer* reached Altai could be quite remote, up to the Neogene. Most likely, *T. nubifer* had been inhabiting the Altai foothills or adjacent regions for not less than several hundred of thousand years. This means that it survived one or more glacial times. The Holocene migration of this species to Altai through arid and semiarid territories seems to be very unlikely. Note that related species of *Triodia* Hübner are absent from Saur-Tarbagatai Mts., separated from Altai by the arid Alakol Depression, and Tien Shan Mts., including the Dzhungarian Alatau, separated from the Saur-Tarbagatai Mts. by an arid depression of Dzungar Gates, although all these mountains are inhabited by such a subnemoral species as *Limenitis helmanni* Lederer, 1853 (but not *L. sydyi* Lederer, 1853!) (Lepidoptera, Nymphalidae) also present in Altai [Lukhtanov, Lukhtanov, 1984; Dubatolov, Kosterin, 2000].

The reason of persistence of a *Triodia* in the Altai-Sayan Mountain System through the Pleitocene

The above considerations seem to lead to a contradiction between inability of existence of a refugium for nemoral and subnemoral flora and fauna in the Altai foothills during the Pleistocene climate coolings, proposed by Dubatolov, Kosterin [2000], and the supposed persistence of *T. nubifer* in Altai, where it had to survive the Pleistocene glaciations. It should be however noted that all nemoral and subnemoral species analyzed by Dubatolov, Kosterin [2000] were species which develop openly on vegetation. R.Yu. Dudko kindly attracted our attention to several species of ground beetles which are endemics of West Altai and are well divergent from their relatives [Dudko, 2011]. These species should have persisted in the Altai Mts. during the Pleistocene coolings and could not get there recently from elsewhere. Thus, factors which have eradicated thermophylous, openly developing from Altai could be less crucial for ground insects able to hide in the soil upper level.

Situation with pedobiotic invertebrates in West Altai in general looks quite different from that with subnemoral Lepidoptera considered by Dubatolov, Kosterin [2000]. For instance, the local fauna of earthworms (Megadrilacea, Oligochaeta, Annelida) includes a number of endemic species from the genus *Eisenia* Malm, 1877, Lumbricidae [Perel, 1979, 1984, 1985; Vsevolodova-Perel, 1997; Blakemore, 2008], like the large *E. magnifica* (Svetlov, 1957), the species with a range in West Altai nearly coinciding with that of *Triodia nubifer* (Fig. 4). Such local endemic species should have survived the Pleistocene coolings *in situ*. That is, among relatively thermophylous animals, pedobiotic ones had more chances to survive in West Altai during the glacial times than openly living ones. Here one should note that the caterpillars of temperate species of moths of the family Hepialidae, to which *T. nubifer* belongs, inhabit soils [Gerasimov, 1952], that is also belong to those pedobionts which should have suffer from climate coolings the least.

Which environmental factors could be most perilous for the thermophylous fauna in the Altai western foothills during the glacial times? The most effective of them could be occasional, sudden and perhaps prolonged frosts in summer. During glacial times, the high mountains of Central Altai were occupied by a huge glacier [Dubinkin, Adamenko, 1968; Okishev, Petkevich, 1988]. In the Middle Pleistocene, when glaciation of Altai reached its maximum, the Ukok Plateau supported an ice shield; the mountains of Upper Biya basin were covered with ice coat, while intermontane depressions of Central and East Altai were filled with ice [Chernov et al., 1998]. Such glaciers must have affected the climate of the surrounding territory through occasional cold winds. The sudden summer frosts could kill insects living openly on vegetation, especially larvae which are unable to actively move and hide. Herpetobiotic insects could easily hide and survive frosts in the soil upper level and under stones. At the same time the pedobionts, including Hepialidae larvae, should be the least vulnerable to sudden frosts. In Hepialidae, the imaginal phase has a short lifespan, so the moth could be able to complete the most vulnerable life cycle stage during frostless periods; besides, the moths are able of active search for shelters. At the same time, the soil-inhabited caterpillars of *Triodia nubifer* should not have been affected at all. Note that because of a very thick snow cover in Gornaya Shoria, the soils in «linden island» do not freeze in winter allowing round the year activity of pedobionts.

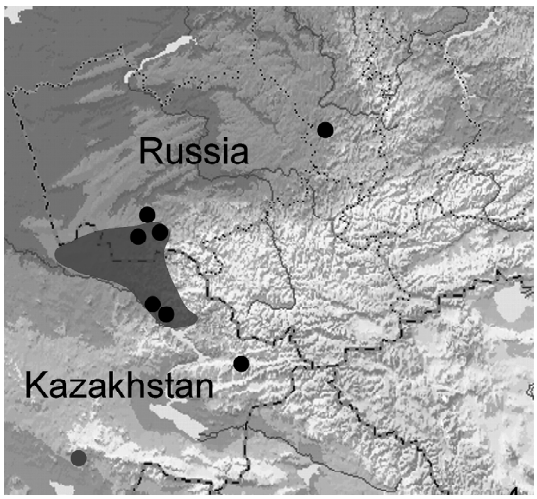


Fig. 4. Distribution of *Triodia nubifer* (Lederer) (black circles) and *Eisenia magnifica* (Svetlov), Lumbricidae, Annelida (gray field and a circle), by Perel, 1984, updated by materials of the Institute of Systematics and Ecology of Animals, Novosibirsk, Russia.

Рис. 4. Распространение *Triodia nubifer* (Lederer) (чёрные кружки) и *Eisenia magnifica* (Svetlov), Lumbricidae, Annelida (серое поле и кружок), по: Перель, 1984, дополнено по материалам Института систематики и экологии животных СО РАН, Новосибирск, Россия.

Conclusions

1. *Triodia nubifer* (Lederer, 1853) (Lepidoptera, Hepialidae) is the only hitherto revealed autochtonous subnemoral species of Lepidoptera in the Altai-Sayan Mountain System which survived one or more climate coolings of the Pleistocene.

2. Nemoral/subnemoral Lepidoptera with openly living larvae, being quite thermophylous, were unable to survive the climate coolings in this area. At the same time, the glacial times were not so ruinous for herpetobiotic and especially pedobiotic nemoral/subnemoral species.

3. Sudden summer frosts probably were the main factor which eliminated the subnemoral Lepidoptera with openly living larvae from the Altai foothills during the glacial times.

Acknowledgements

The authors express their sincere gratitude to Dr. R.Yu. Dudko (Novosibirsk, Russia) for most useful consultations and debating the problem of the article, to Mr. S.A. Knyazev (Omsk) for information about species of the genus *Triodia* Hübner, and to Dr. Zoltan Varga (Hungary) for critical review of the manuscript and valuable comments, and N.B. Ermakov and N.N. Lashchinskiy for consulting on the forest vegetation of Siberia. The study was supported by the Federal Fundamental Scientific Research Program for 2013–2020, Project No. VI.51.1.7 and collaborative research grant No.63 «Phylogeography of insects, birds and mammals of Siberia and the Far East: the history of formation of faunas and contemporary evolutionary trends» by Siberian and Far Eastern Branches of Russian Academy of Sciences.

References

Belyshev B.F., Haritonov A.Yu. 1978. [On latitude and longitude disjunctions in the Eurasian dragonflies (Odonata, Insecta) and their origin] // Izvestiya Sibirskogo otdeleniya Akademii Nauk SSSR. Seriya biologicheskikh nauk. No.5. P.114–188 [In Russian].

Belyshev B.F., Haritonov A.Y. 1981. [Geography of Odonata of Boreal Faunistic Kingdom.]. Novosibirsk, Nauka Press. 297 p. [In Russian].

Blakemore R.J. 2008. An updated list of valid, invalid and synonymous names of Criodriloidea (Criodrilidae) and Lumbricoidea (Annelida: Oligochaeta: Sparganophilidae, Ailoscolecidae, Hormogastridae, Lumbricidae, and Lutodrilidae). 80 pp. [www document]. URL http:// www.annelida.net/earthworm/Lumbricidae.pdf. (Site visited on 27 April, 2014).

Chernov G.A., Vdovin V.V., Okishev P.A., Petkevich M.V., Mistryukov A.A., Zyat'kova L.K., Milyaeva L.S. 1988. [Relief of the Altai-Sayan Mountain Area]. Novosibirsk, Nauka Press. 206 p. [In Russian].

Clarke T.E., Levin D.B., Kavanaugh D.H., Reimchen T.E. 2001. Rapid evolution in the *Nebria gregaria* group (Coleoptera: Carabidae) and the paleogeography of the Queen Charlotte Islands // Evolution. Vol.55. No.7. P.1408–1418.

Dubatolov V.V. 1997. New data on taxonomy of Lycaenidae, Nymphalidae and Satyridae (Lepidoptera, Rhopalocera) of the Asian part of Russia // Far Eastern Entomologist. No.44. P.1–12.

Dubatolov V.V., Knyazev S.A. 2011. [*Triodia nubifer* (Lederer, 1853) (Lepidoptera, Hepialidae) from the Altai Mountains — a new species for the Russian fauna] // Amurian Zoological Journal. Vol.3. No.4. P.367–369. Col. pl.VII–VIII [In Russian].

Dubatolov V.V., Kosterin O.E. 2000. Nemoral species of Lepidoptera (Insecta) in Siberia: a novel view on their history and the timing of their disjunctions // Entomologica Fennica. Vol.11. P.141–166.

Dubinkin S.F., Adamenko O.M. 1968. [Did the Quaternary glaciers of Altai Mountains descend to the regions of their foothills?] // [Kainozoi Zapadnoi Sibiri]. Novosibirsk, Nauka Press. P.65–72 [In Russian].

Dudko R.Yu. 2011. [Relict beetles (Coleoptera: Carabidae, Agyrtidae) with Altai – East Asian disjunctive range] // Euroasian Entomological Journal. Vol.10. No.3. P.349–360, 348. Col. pl.VI. [In Russian, with English Abstract].

Ermakov N. 1998. The Altaian relic subnemoral forest belt and the vegetation of pre-Pleistocene mountainous landscapes // Phytoconologia. Vol.28. P.31–34.

Ermakov N., Dring J., Rodwell J. 2000. Classification of Continental Hemiboreal Forests of North Asia. Département de Botanique et Ecologie de l'Université de Camerino. 180 p.

Freina J. de, Witt Th. 1990. Die Bombyces und Sphinges der Westpalaearktis. Bd. 2: Cossidae, Limacodidae, Megalopygidae, Thyrididae, Hepialidae, Epipyropidae, Heterogynidae. München, Forsching und Wissenschaft. 143 S.

Gerasimov A.M. 1952. [Caterpillars] // Fauna SSSR. Nasekomye Cheshuekrylye. Moscow-Leningrad, Academy of Science of the USSR Press. Vol.1. No.2. 339 p. [In Russian].

Ivonin V.V., Kosterin O.E., Nikolaev S.L. 2012. Butterflies (Lepidoptera, Diurna) of Novosibirskaya Oblast, Russia. 3. Nymphalidae (without Satyrinae). (In Russian, with English Abstract) // Euroasian Entomological Journal. Vol.12. No.2. P.177–199.

Khlonov Y.P. 1965. [Lime and Lime Forests in West Siberia]. Novosibirsk, Nauka Press. 156 pp. [In Russian].

Knyazev S.A., Kosterin O.E. 2003. [New records of nemoral butterflies *Apatura iris* (L., 1758) and *Maniola jurtina* (L., 1758) in West Siberia and their probable zoogeographical significance] // Euroasian Entomological Journal. Vol.2. No.3. P.193–194 [In Russian].

Koropachinskiy I.Yu., Vstovskaya T.N. 2002. [Woody Plants of the Asian Part of Russia]. Novosibirsk, SO RAN Press, Geo Branch. 707 p. [In Russian].

Kosterin O.E., Knyazev S.A., Poteiko A.A., Ponomarev K.B., Kosheleva T.F., Teploukhov V.Yu. 2007. [New records of butterflies (Lepidoptera, Rhopalocera) in Omskaya and Tomskaya Oblast] // Euroasian Entomological Journal. Vol.6. No.4. P.473–482 [In Russian].

Kuminova A.V. 1951. [On the modern state of the lime forest in the Kuznetskii Alatau] // [Proceedings of Tomsk University]. No.116. P.181–186 [In Russian].

Kuminova A.V. 1957. [Teletsky refugium of the Tertiary vegetation.] // [Proc. Eastern Branch of the USSR Academy of Sciences]. Vol.2. P.104–108 [In Russian].

Kuminova A.V. 1960. [Vegetation Cover of the Altai.] Novosibirsk, Nauka Press. 450 p. [In Russian].

Lederer J. 1853. Lepidopterologisches aus Sibirien. // Verhandlungen des zoologisch-botanischen Vereins in Wien. Bd.3. S.351–386. Taf.1–7.

Lukhtanov V., Lukhtanov A. 1984. Die Tagfalter Nordwestasiens. Herbipoliana. Buchreihe zur Lepidopterologie. Bd.3. S.1–440. Herausgeber: Dr. Ulf Eitschberger, Marktleuthen.

Mikkola K. 1987. Pattern of noctuid species common between the extremities of the Palaearctic zone: a result of glacial and postglacial movements. // Tinea. Suppl. Vol.12. P.310–315.

Nielsen E.S., Robinson G.S., Wagner D.L. 2000. Ghost-moths of the world: a global inventory and bibliography of the Exoporia (Mnesarchaeoidea and Hepialoidea) (Lepidoptera) // Journal of Natural History. Vol.34. No.6. P.823–878.

Novák J., Trotsiuk V., Sıkora O., Svoboda M., Chytrı M. 2014. Ecology of *Tilia sibirica* in a continental hemiboreal forest, southern Siberia: an analogue of glacial refugium of broad-leaved temperate trees? // The Holocene. Vol.24. No.8. P.908–918.

Okishev P.A., Petkevich M.V. 1988. [Gornyy Altai] // In: Chernov G.A. (ed.) [Relief of Altai-Sayan Mountain Country]. Novosibirsk, Nauka. P.6–39 [In Russian].

Perel T.S. 1979. [Range and regularities in the distribution of earthworms of the USSR fauna (with keys to Lumbricidae and other Megadrili).] Moscow, Nauka Press. 272 p. [In Russian].

Perel T.S. 1984. *Eisenia magnifica* (Svetlov, 1957) // In: Borodin A.M., Bannikov A.G., Sokolov V.E. et al. (Eds). [The Red Book of the USSR]. Moscow, Lesnaya Promyshlennost' Press. T.1. P.376. [In Russian].

Perel T.S. 1985. Pecularities of the fauna of eathworms (Oligochaeta, Lumbricidae) fauna in Altai refuges of nemorose vegetation // Doklady AN SSSR. Vol. 283. P. 752–755 [In Russian].

Peshkova G.A. 1984. [On the accordance in development of mesophilous and xerophilous florae of the Baikalian Siberia in the Cenozoic] // In: Malyshev L.I. (ed.). [The History of Vegetation Cover of North Asia]. Novosibirsk, Nauka Press. P.144–156 [In Russian].

Pfitzner R. 1912. Family: Hepialidae. // In: Seitz, A. Die Gross-Schmetterlinge der Erde 2: 433–439, Taf. 52–54. Alfred Kernen, Stuttgart.

Polozhii A.V., Krapivkina E.D. 1985. [Relics of the Tertiary Broad-leaved Forests in the Flora of Siberia.] Tomsk, Tomsk Univ. Press. 158 pp. [In Russian].

Reverdatto V.V. 1940. [Main aspects of development of the post-Tertiary flora of Siberia] // Sovetskaya Botanika. Vol.2. P.48–64 [In Russian].

Sinev S.Yu., Zolotuhin V.V. 2008. Hepialidae // In: Sinev S.Yu. (ed.). Catalogue of the Lepidoptera of Russia. St. Petersburg–Moscow: KMK Scientific Press Ltd. P.18–19, 323 [In Russian].

Staudinger O., Rebel H. 1901. Catalog der Lepidopteren des palaearctischen Faunengebiets. Berlin, R. Friedländer & Sohn. T.1. P.I–XLII, 1–411.

Vsevolodova-Perel T.S. 1997. [The earthworms of the fauna of Russia. Cadaster and key.] Moscow, Nauka Press. 102 pp. [In Russian].

Walter, H., Straka, H. 1970. Arealkunde: floristisch-historische Geobotanik. Stutgart, Ulmer. 478 pp.

Yakovlev R., Naidenov A., Artemiev R. 2014: First record of *Apatura iris* (Linnaeus, 1758) in Altai Krai, Russia (Lepidoptera: Nymphalidae) // Entomologist's Gazette. Vol.65. P.11–14.

Zimmerman E.S. 1960. Possible evidence of rapid evolution in Hawaian moths // Evolution. Vol.14. No.1. P.137–138.

Поступила в редакцию 13.10.2014